Quick guide

Naked mole-rat

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What is it? *Heterocephalus glaber* — not exactly cute, but one of the most extraordinary creatures known to science (Figure 1).

What's with the teeth? It looks strange because its lips close behind its teeth; mole-rats are one of the only mammals that can do this. It can spend its entire life underground and forages by tunnelling with its teeth to find tubers. If you were to try digging with your mouth you'd wish you looked more like a naked mole-rat.

It's a mammal Jim, but not as we know it… Mammals are typically characterised as furry and warm-blooded. The naked mole-rat is neither of these. Being underground and surrounded by hundreds of brothers and sisters, there is little fluctuation in surrounding temperature and they have all but lost the ability to regulate their body temperature physiologically. Living in the dark, they can no longer see beyond being able to tell light from dark and they lack pain receptors on their skin. Supremely adapted to their subterranean existence, however, they can run backwards as well as forwards through their tunnels, and can almost somersault within their loose skin, allowing them to manoeuvre around confined spaces. The only hairs on their bodies are specially sensitised to touch, like a cat's whiskers, which allows them to sense the space around them.

Where do they live? In arid areas of eastern Africa where rainfall is infrequent and unpredictable. Tubers are a patchily distributed food source but may weigh as much as 50 kg, are packed with nutrients and, crucially, have a high water content. Naked mole-rats pack soil back into the holes made in the tubers by feeding, so that they can re-grow. Through careful 'farming' in this way, a single tuber can keep a colony alive for a year. This is important because extensive tunnelling is only possible when the ground has been softened by rain.

Wait a minute, did you say a hundred? Yes! In fact, mole-rat colonies can contain up to three hundred animals, living in three kilometres of tunnel. They are extremely social animals and have been studied extensively by biologists keen to discover secrets of how societies stick together. In 1978, entomologist Richard Alexander from the University of Michigan was giving a lecture about eusocial insects. He said if there was a eusocial mammal, it would probably live underground in a harsh environment. Someone at the back put their hand up and said — "I think you're talking about a naked mole-rat". Jennifer Jarvis of Cape Town University on South Africa was studying the naked mole-rat at that time and, since then, others have built on her work to make the naked mole-rat one of the key study species in the social evolution of vertebrates.

So, mole-rats are eusocial; like ants and termites? Yes, eusociality is defined as a social system with castes — physiologically and physically distinct reproductives and non-breeding subordinates; and cooperative care of the young. By this definition, naked mole-rats are the only eusocial mammal, along with its close relative the Damaraland mole-rat. Just like ant colonies, mole-rats have a single reproductive "queen" that produces all the young in the colony with a coterie of two or three breeding males. She can give birth to litters of up to 28 pups, but other colony members will help care for the pups and do the digging and other duties, such as colony defense. Mole-rats take their station in life very seriously and when they meet a colony-mate in a tunnel there is a strict protocol: brief sniffing before the more dominant animal passes by climbing over the top of the subordinate animal. One way that they differ from most eusocial insects is that they are not destined at birth to belong to a specific caste: they can move up the ranks as they age. Living in large social groups may be the only way naked mole-rats can survive in the harsh environment in which they live. There is only a limited time after rain before the ground dries up and becomes too hard for extensive tunnelling and they rely on blind chance to find their food, being unable to detect tubers by smell. A solitary mole-rat would stand a very small chance of blundering into a tuber or patch of tubers.

So is the breeding female the oldest female in the colony? She will be one of the oldest, but that is not her only distinguishing feature.

Figure 1. Cross-section showing digging chain of naked mole-rats (Photo: Justin O'Riain).

When she becomes dominant her body changes so that she becomes physiologically and morphologically distinct from other non-reproductive female 'workers', even her bone structure changes. Mole-rats were thought to be the only mammal to do this, but it has since been discovered that female meerkats also develop elongated vertebra when they become dominant breeders. As well as reproductives, there are also physically and behaviourally distinct dispersive morphs, only known since 1996. Dispersers are big, fat males that try to mate with strange animals from other colonies instead of attack them, as most mole-rats would do. These dispersers are very rare, however, and have never been seen above ground.

So how old is old? Another extraordinary aspect of mole-rat life is that they live to be absolutely ancient relative to their body size. Another rodent of similar size might expect to live for two years; mole-rats have been reported to live for 30 years. They have become of interest to science because of their longevity, as well as their fascinating social behaviour. Because of their extraordinary longevity, scientists expected to find reduced levels of cell-damage and higher levels of anti-oxidant activity in mole-rats, but actually their cell-damage is comparable with that found in other, shorter-lived species. How naked mole-rats survive this cell damage is, as yet, a mystery. It seems we still have a lot to learn from the naked mole-rat.

Where can I find out more?

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Primer

Stereopsis

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"*When I began to see with two eyes, my visual world completely transformed. Trees looked totally different. Consider a leafless tree in winter. Its outer branches enclose and capture a volume of space through which the inner branches permeate. I had no concept of this. Oh, I could infer which branches were in front of others using monocular cues such as object occlusion, but I could not perceive this. Trees to me looked somewhat like a drawing. Before my vision changed I would not have said that the tree looked flat, but I had no idea just how round a tree's canopy really is... When I began to see with two eyes, everything looked crisper and much better outlined. As another formerly stereoblind person wrote to me, 'Everything has edges!' The world was not only flatter but less detailed and textured with my monocular vision*."

The above quotation, from an email contribution by Susan Barry to an on-line discussion of the benefits of stereopsis, eloquently captures many of the perceptual, aesthetic, and even philosophical aspects of 'stereopsis', a word derived from Greek that translates literally as: στερεοσ, 'solid' and οπισ, 'power of sight'. Because Susan Barry acquired this capacity as an adult, she was made vividly aware of what most of us take for granted, namely, a direct sense of the three-dimensionality of the visual world. The quotation also hints at some other critical features of binocular vision that are not related to depth perception *per se*. For example, the statement that "Everything has edges!" attests to the fact that seeing the world twice, as it were, from two slightly different perspectives, makes a number of important visual computations, such as the detection of edges, more robust.

In this primer, we shall mainly deal with stereopsis as narrowly defined, that is, as the use of *differences* in the images projected onto the retinas of the two eyes — so-called 'binocular disparity' — to reconstruct the third visual dimension of depth. We will first describe the basic geometry of binocular disparity before discussing how the brain uses this information to compute depth. We would be remiss, however, if we did not clarify two vital distinctions that place this peculiar capacity within the larger context of vision. The first is that binocular comparisons also serve many other important functions in vision, apart from the computation of depth. The second is that there are many other cues to visual depth that do not require binocular comparisons. Thus, after discussing stereopsis proper, we will briefly treat these two issues.

Basic geometry

Because the two eyes are separated horizontally, they see the same visual scene from two slightly different vantage points. When we 'look at' a particular feature in space, such as the black dot on the arrow in Figure 1A, what we are doing is aiming the fovea — the tiny retinal region of highest visual acuity — of each eye at that feature. This act defines the 'plane of fixation'. If we start at this point on the arrow and move a fixed distance along the gray circle, the projections of the new point in the two eyes will move by *exactly the same distance* on each retina. These points of projection on the two retinas are defined as 'corresponding points'. The geometric horopter is the collection of all such points in the image that project to corresponding points on the retina. (To an observer these points would all appear to lie at roughly the same depth as the point of fixation. The collection of points that appear at *exactly* the same depth is referred to as the "empirical horopter" and is slightly flatter than the geometric horopter.)

Now consider parts of an object that lie either in front of or behind the plane of fixation, such as the head and tail, respectively, of the arrow in figure 1B. These features will not project to corresponding points on the two retinas. That is, the retinal distance from *f* to *h* on the right retina will not be equal to the distance from *f′* to *h′* on the left retina. This difference [(h – f) – (h′ – f′)] is called 'binocular disparity', and it is the basis for stereopsis. The projection lines for retinal points of *near* features cross in front of the horopter and thus produce what are referred to as *crossed* disparities (by convention,